

## CYCLOPYGID TRILOBITES FROM THE ORDOVICIAN OF NORTHEASTERN TARIM, XINJIANG, NORTHWEST CHINA

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### ABSTRACT

Eight species of cyclopygid trilobites are described from the late early Tremadoc and late Llandeilo-early Caradoc of the Queerqueke-Yaerdang mountain area, northeastern Tarim, Xinjiang, China. Three of them are new: *Prospectatrix exquisita*, *Microparia (Heterocyclopyge) abunda* and *M. (Quadratapyge) curva*. The mesopelagic cyclopygids were mainly distributed along the marginal deep facies belt in Tarim, but only some of them were able to penetrate into shallow sites during the period of the great transgression. This indicates that different assemblages of cyclopygid genera may have lived at different depth levels in the water body. Morphological changes which took place during the ontogeny and phylogeny of cyclopygids were minimal, and only a few evolutionary lineages show local heterochronic evolution.

### INTRODUCTION

The material on which this paper is based was mainly collected by the Regional Geological Surveying Team of Xinjiang during the last decade from the Queerqueke-Yaerdang Mountain area on the north bank of the Konqi River (Figure 1). The Ordovician lithostratigraphy in this area was erected by Norin (1937). Since then, however, more detailed information has been added (Zhou *et al.* in Zhou and Chen 1990; Zhong and Hao, 1990). Ordovician trilobites were partly described by Troedsson (1937) and Zhang (1981), but no cyclopygids had been reported from the vast northeastern area of Tarim until 1990, when a few specimens were recorded by Zhou (in Zhong and Hao 1990). In this paper eight species of cyclopygid trilobites in the genera and subgenera *Prospectatrix*, *Pricyclopyge*, *Cyclopyge*, *Microparia (Microparia)*, *Microparia (Heterocyclopyge)*, *Microparia (Quadratapyge)*, *Degamella* and *Sagavia* are formally described, including three new species.

The terminology used in the ensuing taxonomic descriptions is essentially that defined by Harrington *et al.* (in Moore 1959: 117-126), except that the occipital ring is considered as part of the glabella, as no occipital ring is defined in any cyclopygids, even in the ellipsotaphrines (Fortey and Owens 1987: 188).

Specimens described in the following pages are all deposited at the Nanjing Institute of Geology and Palaeontology, Academia Sinica (NI).

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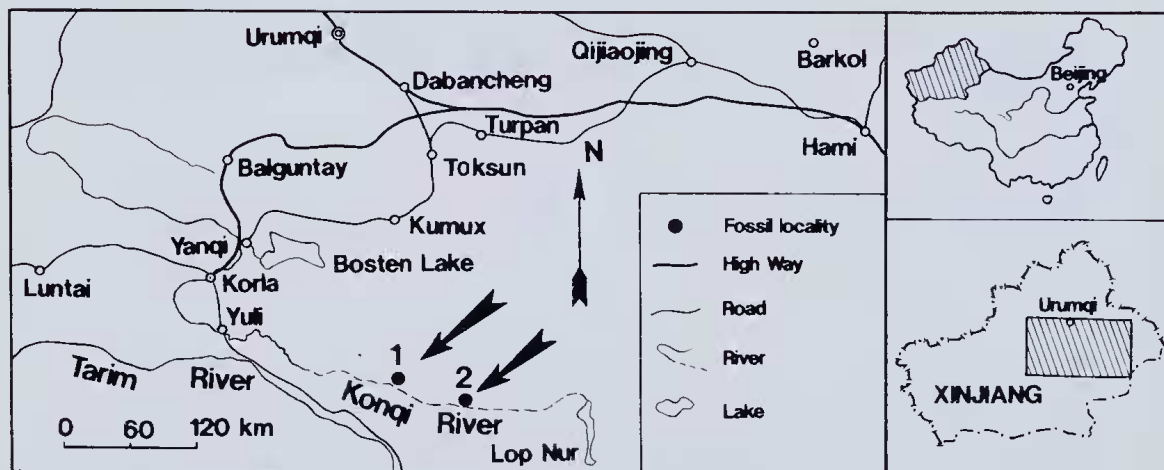


Figure 1 Sketch map showing the fossil localities. 1. Queerqueke; 2. southern Yaerdang.

### Stratigraphy and age

All the cyclopygid trilobites described in this paper were collected from the measured section at Queerqueke ( $40^{\circ}54'N$ ,  $88^{\circ}18'E$ ) (locality 1) except for a few additional specimens which were gathered from south Yaerdang ( $40^{\circ}45'N$ ,  $89^{\circ}02'E$ ) (locality 2). They occur in three separate horizons and, according to Zhou *et al.* and Lin *et al.* (in Zhou and Chen 1990), the stratigraphic setting and other associated fossils are as follows:

1. The primitive cyclopygid *Prospectatrix exquisita* sp. nov. is the only form to appear at both localities, where it is found in a bed of greyish black thin-bedded argillaceous and nodular limestones of the upper part of the Torsuqtagh Group, which is 12m thick at Queerqueke and 23m thick at south Yaerdang. The other trilobites from this horizon include *Bienvillia cavernosa* Lisogor, *B. tetragonalis* (Harrington), "*Pseudoperonopsis*" *oblonga* Lu and Lin, *Dichelepyge sinensis* Lu and Lin, *Borthaspidella anderssoni* (Troedsson) and *Niobella preciosa* (Lu and Zhou), indicating the *Dichelepyge sinensis* Zone. Lu *et al.* (1984, Table 1), considered that the *D. sinensis* Zone can be roughly correlated to the *Adelograptus tenellus* graptolite Zone of the British standard zonation. The conodonts found in association with the trilobites are, *inter. al.* *Cordylodus angulatus* Pander, *C. rotundatus* Pander and *Drepanodus tenuis* Moskalenko, indicative of the *Cordylodus angulatus* Zone of late early Tremadoc age.

2. The most diverse cyclopygid assemblage in our collection makes its appearance at Queerqueke in the middle part of the Charchaq Group, a bed of rhythmic greyish green siltstones, shales and thin-bedded calcarenites, 400m in thickness; it comprises up to seven species: *Pricyclopyge* cf. *binodosa longicephala* Klouček, *Cyclopyge* cf. *recurva* Lu, *Microparia* (*Microparia*) sp., *M. (Heterocyclopyge) abunda* sp. nov., *M. (Quadratapyge) curva* sp. nov., *Degamella* cf. *princeps* (Barrande) and *Sagavia felix* Koroleva. Other trilobites found in the same bed were identified by the authors as *Dionide* sp., *Illaeopsis* sp., *Girvanopyge* sp., *Birmanites* sp. and *Lonchodomas* sp. The associated graptolites include, among others, *Nemagraptus gracilis* (Hall), *Corynoides pristinus* Ruedemann, *Dicranograptus brevicaulis* Elles and Wood, *Dicellograptus sextans exilis* Elles and Wood, *Cryptograptus tricornis* (Carruthers) and *Climacograptus brevis* Ellis and Wood, suggestive of the

*Nemagraptus gracilis* Zone, which is considered to be late Llandeilo to earliest Caradoc in age.

3. Two cyclopygids, that is, *Cyclopyge* cf. *recurva* Lu and *Microparia* (*Heterocyclopyge*) *abunda* sp. nov., extend upwards from the *Nemagraptus gracilis* Zone to an overlying bed of the Charchaq Group at Queerqueke, which is composed of variegated clastic sandstones and siltstones intercalated with calcareous shales, 350m in thickness. This has yielded graptolites, including *Climacograptus bicornis* (Hall), *C. minimus* (Carruthers), *Dicranograptus sinensis* Ge, *D. brevicaulis* Elles and Wood, *Pseudoclimacograptus scharenbergi* (Lapworth), *Dicellograptus sextans exilis* Elles and Wood, *D. pumilus* Lapworth and *Orthograptus calcaratus* Lapworth. All may belong to the *Climacograptus bicornis* Zone and indicate an early Caradoc age. One more cyclopygid has been found in this horizon by Zhong and Hao (1990: 120, pl.5, fig.13), and identified as *Ellipsotaphrus* sp. by one of the authors (Z.Z.).

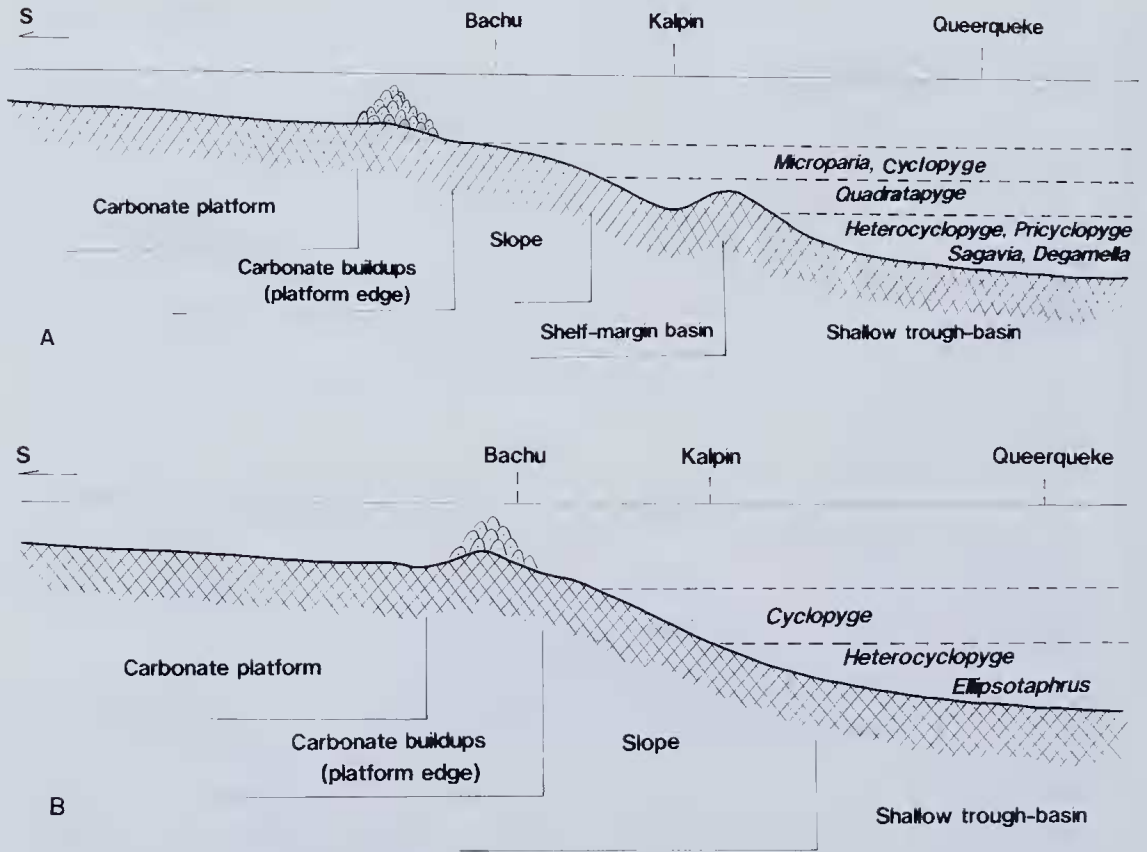
### Pattern of distribution

As pointed out by Zhou *et al.* (in Zhou and Chen 1990), during the Ordovician the vast expanse of the Tarim Block was a shallow-water carbonate platform with the water body gradually deepening northwards. The evidence from the lithofacies and biofacies demonstrates that a marginal basin (Tremadoc-early Arenig) or trough (middle Arenig-early Ashgill) existed along the present north margin of the block, and the Queerqueke-Yaerdang mountain area may have formed part of the exterior marginal belt.

According to Zhou *et al.* (in Zhou and Chen 1990), cyclopygids have hardly ever been found in the platform (for example, the Bachu area) or even in the shelf (for example, the Kalpin area) deposits in Tarim, except from late Llandeilo-Caradoc rocks when transgressive sedimentary regimes were progressively introduced worldwide (cf. Fortey 1984). During this great transgression a few cyclopygid forms penetrated over the former shallow shelf and became more widely distributed. In the period of the *Nemagraptus gracilis* Zone (Figure 2A) *Cyclopyge* cf. *recurva* Lu and *Microparia* (*Microparia*) *acuta* Zhang occur in a Nileid Association of shelf slope facies in association with *Nileus convergens* Lu, *Peraspis* sp., *Poronileus* sp., *Lonchodomas* sp., *Dividuagnostus* sp. and *Birmanites* sp., while *Cyclopyge* sp., *Microparia* (*Microparia*) sp., *M. (Quadratapyge) chedaoensis* Zhou and Dean and *M. (Q.)* sp. appear in the shelf-margin basin deposits together with various graptolites and other trilobites of a Shumardiid Biofacies, including *Lisogorites tarimensis* Zhang, *Dividuagnostus* sp., *Taklamakania xinjiangensis* Zhang, *Ampyx yohi* Lu, *Shumardia tarimuensis* Zhang, *Telephina angulata* (Yi), *Peraspis obscura* Zhou and Dean, *Birmanites* sp. and *Endymionia circularis* Zhang. In the interval of the *Climacograptus bicornis* Zone (Figure 2B) *Cyclopyge* cf. *recurva* Lu alone was found in a upper slope facies limestone bed in the Kalpin area; the other trilobites from this horizon include *Nileus convergens* Lu, *Birmanites kanlingensis* Zhang, *Stenopareia* sp., *Ampyx* sp., *Ovalocephalus* sp., *Dionide* sp. and *Corrugatagnostus* sp., suggestive of another Nileid Association. It is interesting to note that some cyclopygids, such as *Microparia* (*Heterocyclopyge*), *Pricyclopyge*, *Sagavia* and *Ellipsotaphrus*, which flourished in the deeper water site never occurred in the shallower water site. *M. (Quadratapyge)* never spread into the shallower shelf.

The occurrence of *Prospectatrix* in late early Tremadoc in Tarim suggests that from their earliest occurrence the Cyclopygidae had a very wide distribution, extending from Europe across Asia. Kobayashi and Hamada (1970) considered that the earliest cyclopygids in Asia were Middle Ordovician in age. But the presence of *Prospectatrix* in Europe and Asia in the Tremadoc argues for a rapid radiation around much of marginal Gondwana.

Cyclopygid trilobites from northwest China



**Figure 2** Palaeogeographic profiles across the Tarim Block (after Zhou *et al.* in Zhou and Chen 1990) showing the depth differentiation of the mesopelagic cyclopygids during the late Llandeilo-earliest Caradoc (A) and early Caradoc (B).

Fortey (1985) and Fortey and Owens (1987) considered the cyclopygids to be mesopelagic trilobites living above the lower limit of the photic zone, or at a depth of 200–700m below the water surface. The distributional pattern of cyclopygids in Tarim reveals that most of them were only distributed along the continental margin at a water level of considerable depth. However, a few genera, such as *M. (Quadratapyge)*, may have lived at shallower, but sufficiently deep, water levels to have been able to invade onto the shelf basin, or even, in the case of *Cyclopyge* and *M. (Microparia)*, onto the interior shelf slope. It seems likely, therefore, that there may have been a depth-induced ecological differentiation between the morphologically similar cyclopygid genera.

## ONTOGENY AND HETEROCHRONY

### Ontogeny

Aspects of the ontogenetic development of cyclopygids have been mentioned by a number of authors. The ontogeny of *Cyclopyge* has been discussed by Marek (1961), Tripp *et al.* (1989) and Kielan (1959); *Microparia* and *Heterocyclopyge* by Marek (1961), who along with

Barrande (1872) and Whittard (1961) discussed features of the ontogeny of *Degamella*. The ontogeny of *Pricyclopyge* was also covered, in part, by Marek (1961) and Whittard (1961), along with Rushton and Hughes (1981). Six of the species descriptions provided herein are based on both meraspid and holaspid material. Consequently ontogenetic changes that occurred in these six species have been documented and are found to involve 11 different morphological features. In two species, *Cyclopyge* cf. *recurva* and *Degamella* cf. *princeps*, the glabella elongated and narrowed anteriorly, whereas in *Pricyclopyge* cf. *binodosa longicephala* it broadened during ontogeny. In the latter species there was also a narrowing of the fixigena. In *Cyclopyge* cf. *recurva* and *Microparia* (*Heterocyclopyge*) *abunda* the palpebral lobe narrowed and became convex during ontogeny. In *C.* cf. *recurva* the visual surface of the eye enlarged by an increase of longitudinal files of lenses.

Deepening of the pygidial border furrow is a common feature in the ontogeny of these cyclopygids and was often associated with a widening of the border, which became more well-defined in later meraspids and holaspids. This occurred in *Pricyclopyge* cf. *binodosa longicephala*, *Cyclopyge* cf. *recurva*, *Microparia* (*Heterocyclopyge*) *abunda*, *Microparia* (*Quadratapyge*) *curva* and *Sagavia felix*. On the contrary, effacement of pygidial pleural and interpleural furrows occurred in *Pricyclopyge* cf. *binodosa longicephala* and *Sagavia felix*. Other ontogenetic changes that occurred in the pygidium were, among others, the widening of the axial rings in *Cyclopyge* cf. *recurva*, and the deepening of the axial furrow and development of the postaxial groove in *Microparia* (*Quadratapyge*) *curva*. In addition, the true pygidium, semicircular in early growth stages, tended to become triangular in late stages in *Pricyclopyge* cf. *binodosa longicephala*.

### Heterochrony

Variations in the extent of ontogenetic changes between cyclopygid species enables the role of heterochrony in the evolution of this group of trilobites to be evaluated. It is probably no surprise, given the relatively minor morphological changes that occurred during ontogeny in cyclopygids, that morphological differences between cyclopygid species are correspondingly relatively slight. Hence the observation of Fortey and Owens (1987:151) that “many cyclopygid genera .... are extraordinarily conservative”. Whereas they ascribe this conservatism to the stable, offshore environment in which the cyclopygids lived, we believe that it is, to a large degree, a reflection of the small degree of ontogenetic change that took place during the ontogeny of species within this family. This is the opposite situation to the case in many Cambrian trilobites (McNamara 1986) wherein the large scale ontogenetic changes engendered a wide range of interspecific heterochronic morphotypes.

Whereas in Cambrian trilobites the incidence of progenesis, arising from premature sexual maturation, was a relatively common phenomenon (McNamara 1983), it was of only relatively minor importance in cyclopygids. Fortey (1981) and Fortey and Owens (1987) consider *Prospectatrix* to be the most primitive cyclopygid and to have been derived from a Nileid-like ancestor, as suggested by the small eyes and retention of the broad fixigenal area and cephalic median suture. This proposed relationship is strengthened by the discovery of an elongate median glabella tubercle in *Prospectatrix exquisita* sp. nov. The presence of this feature was not recorded in the type species of *Prospectatrix* by Fortey (1981).

The type species of *Prospectatrix* possesses seven thoracic segments (although the new species described herein has only six), and in this regard is comparable with many Nileids. Cyclopygid genera, such as *Microparia* and *Sagavia*, that possess only 5 thoracic segments,

are therefore relatively paedomorphic and are likely to have arisen by progenesis, as indeed would have species such as *Prospectatrix exquisita* sp. nov.

Minor local heterochronic changes in cyclopygids have previously been recognised by Fortey and Owens (1987). Of relevance to the material described in this paper, they note that the gradual change in shape of the glabella through a number subspecies of *Pricyclopyge binodosa*, from *eurycephala-binodosa/prisca-longicephala*, involves heterochrony, although they did not specify, whether by paedomorphosis or peramorphosis. The ontogenetic changes documented herein in *P. cf. binodosa longicephala* (Figures 3E, 5A,E) may allow the polarity of these changes to be assessed. The earliest form *P. binodosa eurycephala*, as its name implies, has a very broad cranium, with the maximum width posterior to the cranial mid-length. Although the glabella of *P. cf. binodosa longicephala* widened during ontogeny, it attained the maximum width much more anterior than in *P. binodosa eurycephala*. The shape of the late meraspid glabella of *P. cf. binodosa longicephala* is, in turn, similar to that of the early meraspid juveniles of *P. binodosa binodosa* illustrated by Rushton and Hughes (1981, pl.2, figs 20, 22, 23). Consequently, it can be argued that the three subspecies in question can be regarded as forming a paedomorphocline in this character.

*Pricyclopyge* is morphologically close to the primitive cyclopygid *Prospectatrix*, from which it may have been derived. The larger eyes of *Pricyclopyge* suggest a peramorphic increase in lens number from *Prospectatrix*. The rounded holaspid pygidium of *Prospectatrix* (Figure 3A) is reminiscent of the juvenile pygidium in *Pricyclopyge*, before it becomes acuminate posteriorly. This change in pygidial shape in *Pricyclopyge* is therefore also a peramorphic feature.

The cyclopygid species described in this paper that shows most ontogenetic change is *Cyclopyge cf. recurva* Lu in Wang, 1962 (Figure 4). These include a lengthening of the glabella, which became more narrowly rounded anteriorly (Figure 4C,G-I); the palpebral lobe is narrow (tr.) and wire-like in adult, but more flattened and wider (tr.) in juvenile specimens (Figure 4C,I); the pygidial border is absent until degree 3 (Figure 4C), but then gradually became more markedly defined (Figure 4H) and wider (sag.); the visual surface of the eye was enlarged by the increase of longitudinal files of lenses; axial rings widened (tr.); and the length/width ratio was much reduced from the transitory to the holaspid pygidium.

In primitive species of *Cyclopyge*, such as *C. grandis grandis* (Salter, 1859) (Fortey and Owens 1987: 151) the pygidial axis is long and segmented, while the eyes are separated anteriorly. In later species, such as *C. cf. recurva* described herein (see also Zhou and Dean 1987) and also later Ordovician forms such as *C. rotundata* Lu (see Tripp *et al.* 1989); *C. mirabilis* (Forbes MS in Salter, 1853) (see Whittard 1952); *C. vigilans* (Cooper and Kindle, 1936); *C. marginata* Hawle and Corda, 1847 (= *C. quadrangularis* Kielan, 1959: 83), the pygidial axis is short, including only one ring in large specimens. This is therefore a paedomorphic character in these later species. The eyes, however, became fused anteriorly in later species as the number of lenses increased by peramorphosis. The broader pygidial border of these later species is another peramorphic character. Marek (1961) has shown how the pygidial border is not developed in meraspid of *C. marginata*, but is wider and more defined in holaspids of *C. rotundata* (see Tripp *et al.* 1989).

Species of *Degamella* show an appreciable variation in eye size. For example, Fortey and Owens (1987: 160) have noted that the Llanvirn – Llandeilo *D. princeps* (described herein) has a surprisingly small eye for a cyclopygid, being smaller than in the late Arenig form *D. evansi* Fortey and Owens, 1987. Eyes in the Ashgill species *D. gigatea* (Barrande) (Marek

1961: 49, pl. 5, figs 1–3) are even smaller than *D. princeps*. Such eye reduction is likely to have occurred by pedomorphosis, and is somewhat at variance with the general trend for peramorphic increase in eye size in cyclopygids as a whole.

It has been suggested (Marek 1961; Fortey and Owens 1987) that *Degamella* and *Microparia* are closely related. The meraspid *Degamella* has a much wider glabella than the holaspid, and in this regard resembles the holaspids of *Microparia*. Fortey and Owens (1987: 172) have observed the similarity of the cranidium of a degree 5 meraspid of *D. nuda* (Whittard, 1961), and the holaspid of *M. teretis* Fortey and Owens, 1987. If *Degamella* is considered to have evolved from *Microparia*, then the narrowing of the glabella through ontogeny in *Degamella* would be a peramorphic feature.

Fortey and Owens (1987: 177) considered that the similarity in structure of the pygidial axis of *Sagavia*, *Microparia* and *Degamella* indicated a common ancestry. The increase in axial length and definition during the ontogeny of *Sagavia* (see herein Figure 8A–J), compared with the effacement that occurred during ontogeny in some species of *Microparia*, suggests that the evolution of the pygidial axis in *Sagavia* occurred by peramorphosis.

#### *Ecological significance of heterochronic morphological changes*

Many of the morphological changes that occurred in cyclopygids by heterochrony can be explained in terms of selection for particular morphologies that were particularly suited to a pelagic existence. The specific morphological features that so typify cyclopygid trilobites, notably the broad axis, including the glabella, and the greatly enlarged eyes, arose by local peramorphic changes to growth allometries and rates of lens production. The massive eyes that were so produced greatly improved the visual area and were of strong selective advantage to pelagic trilobites. Those cyclopygids, such as *Degamella* and *Cyclopyge*, that underwent peramorphic elongation of the glabella, probably reflect selection for more active swimming morphologies (Fortey 1985).

The subsequent changes to these characters within particular lineages were relatively small and occurred over long time periods. Thus the generic assemblage of cyclopygid trilobites is very similar from the Arenig to the Ashgill. This morphological conservatism derives both from the stable environment that they inhabited, but also from the relatively small allometric changes that occurred during ontogeny, restricting the capacity for the evolution of heterochronic morphotypes.

## SYSTEMATIC PALAEOONTOLOGY

### Family Cyclopygidae Raymond, 1925

#### Genus *Prospectatrix* Fortey, 1981

#### Type species

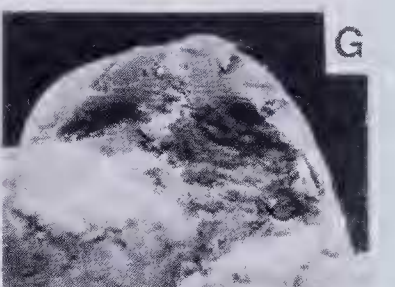
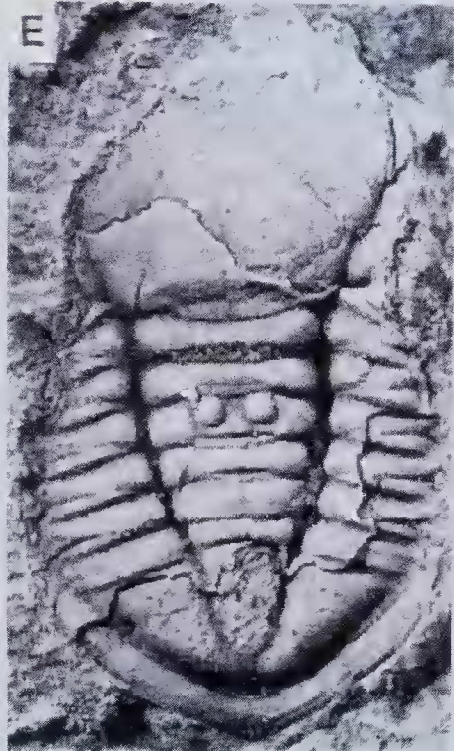
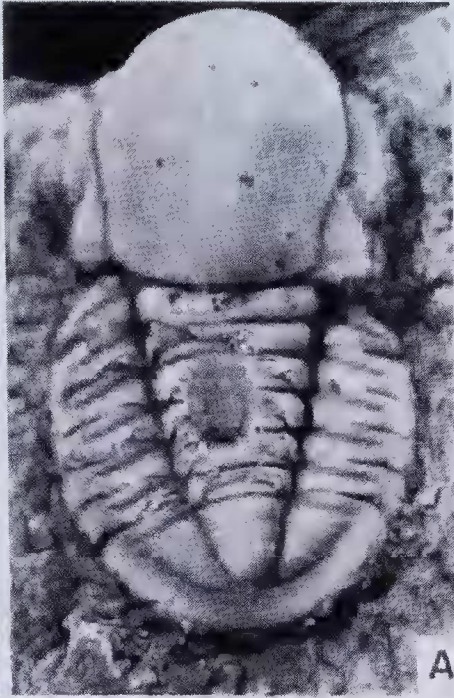
*Cyclopyge genatenta* Stubblefield in Stubblefield and Bulman 1927, from the *Shumardia* (*Conophrys*) *salopiensis* Zone of the Shineton Shales (upper Tremadoc), Shineton, Shropshire, England.

#### *Prospectatrix exquisita* sp. nov.

Figure 3A–D, F–I

*Prospectatrix* sp., Zhou in Zhong and Hao, 1990: 118, pl. 5, figs 14, 15.

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## Etymology

Latin *exquisitus*, a, um, excellent, referring to the well preserved type specimens.

## Holotype

Dorsal shield lacking librigenae, NI 120569 (Figure 3A–C), from the *Dichelepyge sinensis* Zone of the upper part of the Torsuqtagh Group, locality 1.

## Paratypes

One incomplete cephalon (NI 120570) and one left eye (NI 120572) (locality 2), and one right librigena (NI 120571) (locality 1), all from the *Dichelepyge sinensis* Zone of the upper part of the Torsuqtagh Group.

## Diagnosis

A species of *Prospectatrix* with six thoracic segments. Palpebral area of fixigena 14% width and 50% length of glabella; posterior area about 20% basal width of glabella. Pygidial axis with two rings defined by shallow ring furrows. Pygidial border furrow distinct.

## Description

Dorsal shield oval in outline, 60% as wide as long; cephalon 45%, thorax 33%, and pygidium 22% the exoskeletal length. Cranidium wider than long. Glabella large, strongly convex, 90% as wide as long, broadly rounded and overhanging preglabellar furrow anteriorly, slightly constricted opposite the posterior pair of glabellar depressions, from where it expands forward to a maximum width at 44% glabellar length from front, nearly at the level of the median tubercle; three pairs of faint isolated oval depressions present on the flanks, successively becoming smaller anteriorly; only posterior lateral glabellar furrow well defined in some specimens, being eyebrow-shaped, extending along the anterior margin of the posterior depression; median tubercle elongate, shown only on testaceous surface, but absent in exfoliated specimens. Axial furrow sigmoid, deeply incised. Fixigena narrow (tr.), low, gently convex, turning downwards abaxially; palpebral area of fixigena 14% width of the glabella in plan; palpebral lobe strip-like, convexly curved abaxially, about 50% the glabellar length, alongside axial furrow anteriorly; palpebral furrow absent; posterior area of fixigena small, triangular, more than 20% the basal width of the glabella; posterior border short (exsag.), well demarcated by shallow border furrow. Posterior sections of facial sutures diverge backwards; anterior sections extending along axial furrows and meeting at sagittal line in front of the glabella. Librigena mainly composed of large eyes, which are recurved, strongly convex, with lenses hexagonally arranged, reducing in size ventrally; anterior to eye genal field narrowing forwards; median part of doublure crescentic in outline, rounded anteriorly, separated by median suture, covered with about 10 terrace lines roughly parallel to the

◀ **Figure 3** A–D, F–I, *Prospectatrix exquisita* sp. nov., from the *Dichelepyge sinensis* Zone of the upper part of the Torsuqtagh Group; A–C, dorsal shield lacking librigenae, holotype, dorsal, lateral, anterior views, NI 120569, x5, Loc.1; D, F, G, cephalon, paratype, dorsal, lateral, ventral views, NI 120570, x5, Loc.2; H, right librigena, paratype, latex cast from external mould, NI 120571, x15, Loc.1, 1, left eye, paratype, NI 120572, x10, Loc.2. E, *Priocyclopyge* cf. *binodosa longicephala* Klouček, 1916, incomplete dorsal shield of degree 5, NI 120573, x10, from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, Loc.1.

posterior and lateral margins, tapering sharply backwards into narrow bands that extend along ventral margins of eyes.

Thorax of six segments. Axis convex (tr.), well defined by deep and broad axial furrows, tapering backwards; articulating half ring widely rounded anteriorly, more than 35% length of ring; articulating furrow deep and wide. Pleurae broadly rounded laterally, first pleura shortest, about 40% the axial width, progressively widening posteriorly to the fourth segment and similar width thereafter, including a horizontal proximal part adaxial to fulcra and a downwardly bent faceted distal part abaxial to fulcra; fulcrum of sixth segment placed at 40% its pleural width from axial furrow, becoming slightly successively closer to the axial furrow in preceding segments; pleural furrow deeply incised, narrowing abaxially, dying out before reaching lateral margin; pleura uniform in width with truncated extremity except the first segment which is triangular in form and ends in a short point; facet triangular, wide (tr.).

Pygidium 50% as long as wide, semicircular in shape. Axis strongly convex, 32% the anterior width and 65% the length of the pygidium, narrowing steadily backwards, narrowly rounded posteriorly, including two rings defined by shallow ring furrows, and a terminal piece in addition to an articulating half ring; postaxial ridge short, extending from the rear end into the pygidial border. Pleural lobe gently convex; anterior half pleura narrowing adaxially, faceted anterolaterally, well delimited by deep pleural furrow. Border wide (sag.), uniform in width, low, flat. Border furrow well defined by change of convexity from pleural lobe to border.

Surface of cranium, thorax and pygidium covered with fine anastomosing raised lines, mainly transversely extended but subparallel to the nearest exoskeletal margins peripherally. Similar lines are absent from the central glabellar part round the median tubercle, the lateral glabellar depressions, the posterior area of the fixigena and the palpebral lobe.

## Discussion

Except for the type species, other forms referred to the genus *Prospectatrix* have been described from the late Tremadoc of the western Lake District, England (Rushton 1988), the early Arenig of the Taurus Mountains of Turkey (Dean 1973), and the Fennian (late Arenig) of South Wales (Fortey and Owens 1987). Additionally, a cranium illustrated by Apollonov *et al.* (1984, pl.23, fig.11) from the Malyi Karatau Range, Kazakhstan may also referable to this primitive cyclopygid genus, as indicated by Rushton (1988: 694).

The new species closely resembles the type species *P. genatenta* (Stubblefield) (Stubblefield and Bulman 1927: 138, pl.4, figs 9–11; Fortey 1981: 611, pl.1, figs a–j), but differs in having six instead of seven thoracic segments, in the narrower posterior area of fixigena (20% vs. 30% the basal width of the glabella), in the longer palpebral lobe (50% vs. 36% the glabellar length) and in the shallower ring furrows but more distinct border furrow of the pygidium. It also differs in possessing an elongate median glabellar tubercle. These diagnostic features of the present species are in turn compatible with those of *P. superciliata* (Dean 1973: 314, pl.6, figs 2, 4, 6, 8, 9, 14), but the Turkish species displays a glabella steadily expanded forwards with no constriction opposite the 1p glabellar depressions, and its palpebral area of fixigena is slightly narrower (tr.) (11% vs. 14% the glabellar width in plan).

A juvenile pygidium described as Cyclopygid? gen. and sp. undet. by Dean (1973: 316, pl.6, fig.3) from the late Arenig of the Taurus Mountains, Turkey seems assignable to *Prospectatrix*; it is comparable with that of *P. exquisita*, especially in the deep pygidial border furrow, although it is longer. *P. brevior* Rushton (1988: 694, pl.68, figs 1–3) has a wider

posterior area of fixigena that is similar in size to that of the type species, a very narrow (tr.) but shorter (exsag.) palpebral area of fixigena and a longer pygidium showing three axial rings; otherwise it is close to the new species.

*Prospectatrix* sp. (Zhong and Hao 1990) was recorded from the same locality and horizon as the holotype of this species. The characteristic features coincide well with each other, and we consider both as conspecific.

### Genus *Pricyclopyge* Richter and Richter, 1954

#### Type species

*Aeglina prisca* Barrande, 1872, from the Šárka Beds (Llanvirn), Bohemia.

### *Pricyclopyge* cf. *binodosa longicephala* Klouček, 1916

Figures 3E, 5A,E

#### Figured specimens

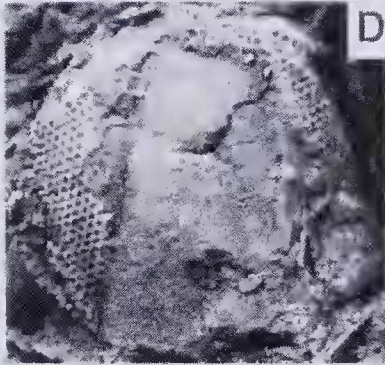
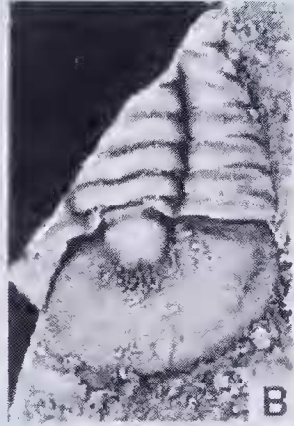
Three dorsal shields (lacking librigenae) of degrees 5 (NI 120573), 2 (NI 120575) and 1 (NI 120574), all from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, locality 1.

#### Discussion

No mature specimens have been found in our collection, but the incomplete carapace of degree 5, 8mm in length, bears a great resemblance to the lectotype of *P. binodosa longicephala* Klouček, 1916 (see Marek 1961: 34, pl.1, fig.21) from the Dobrotivá Beds (Llandeilo), Malé Přílepy, near Beroun, Bohemia; the glabella is slightly shorter, but, as noted by Marek (1961: 34), the length/width proportion may vary in the subspecies of *P. binodosa*, especially if specimens are preserved in shales and more or less compressed. Judging from the anterior glabella margin which is gently forwardly convergent and a pair of slender spines shown on the anterior unliberated segment (future sixth thoracic segment), the present material may probably be referred to *P. binodosa longicephala*, but further adult specimens are required before we make a definite conclusion. With regard to the shape of the glabella and pygidium, this form is also comparable with *P. compesteris* Koroleva, 1967 (see also Koroleva 1982: 124, pl.25, fig.12) from the Llandeilo of northern Kazakhstan, but the terminal spines of the sixth thoracic segment seems slightly thicker in the latter. Fortey and Owens (1987: 184) have implied that the Kazakhstan species may be synonymous with the contemporaneous Bohemian species.

The degree 2 dorsal shield is about 4mm long. The glabella is pear-shaped, 80% as long as wide, with greatest width at 66% the glabellar length from the posterior margin. The fixigena is triangular, about half the basal glabellar width, and tapers forwards. The palpebral lobe is long, narrow and rim-like, and posteriorly extends just to the anterior margin of the posterior area of the fixigena. The transitory pygidium, about 85% as long as wide, shows slightly forwardly convergent lateral margins, but is broadly rounded posteriorly. The true pygidium has faintly furrowed pleural lobes but no well defined border furrow. The degree 1 dorsal shield, 3mm long, is similar to that of degree 2, but the transitory pygidium is longer (as long as wide). A pair of hollow nodes which is well defined on the axial ring of the third thoracic

Cyclopygid trilobites from northwest China



segment is not seen on the axis of the degree 1 and 2 transitory pygidia. This is obviously owing to the poor preservation of these specimens.

According to the present incomplete growth series, the morphological changes during the meraspid period of this form may comprise the narrowing of the fixigenae, the deepening of the pygidial border furrow, the effacement of the pygidial pleural and interpleural furrows, and the broadening of the glabella and transitory pygidium. Furthermore, the shape of the true pygidium is triangular in degree 5 but semicircular in smaller specimens.

Similar morphological changes are also exhibited in the size series of *P. binodosa binodosa* (Salter in Murchison 1859), as described by Whittard (1940, 1961) and Rushton and Hughes (1981). Specimens of degree 1 in this European species (Rushton and Hughes 1981: 633, pl.2, figs 20, 23, 24), as compared with those at the same stage in the present form, display a slightly wider (tr.) palpebral area of fixigena. The dorsal shield shown by Rushton and Hughes (1981, pl.2, fig.22) may probably represent that of a degree 2 specimen, which differs in the broader glabella and better defined pygidial border furrow. The deeply incised pygidial border furrow and the more narrow anteriorly rounded glabella seen in holaspids of *P. binodosa binodosa* (Whittard 1961, pl.23, fig.16) appeared between meraspid degrees 2 and 3.

### Genus *Cyclopyge* Hawle and Corda, 1847

#### Type species

*Egle rediviva* Barrande, 1846, from the Černin Beds (Caradoc) of Trubin, near Beroun, Bohemia.

### *Cyclopyge* cf. *recurva* Lu in Wang, 1962 Figure 4A–I

*Cyclopyge* cf. *recurva* Lu, Zhou in Zhong and Hao, 1990: 119, pl. 5, fig. 12.

#### Figured specimens

One cephalon (NI 120576), three incomplete dorsal shields (NI 120580, 120581, 120582), one incomplete pygidium with attached thorax (NI 120577), one degree 2 dorsal shield (NI 120578) and one degree 5 dorsal shield (lacking librigenae) (NI 120583) from the *Climacograptus bicornis* Zone, and one cephalon (NI 120579) and one degree 3 dorsal shield (lacking librigenae) (NI 120584) from the *Nemagraptus gracilis* Zone, of the middle part of the Charchaq Group, locality 1.

#### Description

##### *Holaspid stage*

Dorsal shield elliptical in outline, about 6–7.5 mm long in the collection; cranium 46%, thorax 28% and pygidium 26% the exoskeletal length. Glabella convex, tapering forwards,

◀ **Figure 4** A–I, *Cyclopyge* cf. *recurva* Lu in Wang, 1962, A–C, E–H, from the *Climacograptus bicornis* Zone, D, I, from the *Nemagraptus gracilis* Zone, of the middle part of the Charchaq Group, Loc.1; A, cephalon, NI 120576, x10; B, pygidium attached with incomplete thorax, NI 120577, x10; C, dorsal shield of degree 2, NI 120578, x15; D, cephalon, NI 120579, x10; E, incomplete dorsal shield, NI 120580, x8; F, dorsal shield lacking librigenae, NI 120581, x10; G, dorsal shield, NI 120582, x10; H, dorsal shield lacking librigenae, degree 5, NI 120583, x10; I, dorsal shield lacking librigenae, degree 3, latex cast from external mould, NI 120584, x15.

rounded anteriorly, almost as long as wide. 1p glabella furrow elongated, pit-like, abaxial extremity placed at 30% of glabella length from posterior margin, from there it extends inwards and backwards. A pair of circular swellings situated just posterior to the glabellar furrows. Median tubercle in line with anterior margin of 1p furrows. Palpebral lobe narrow, convex, wire-like, extending along glabella, well defined by deep and wide axial furrow. Posterior area of fixigena triangular, tiny. Librigenae united; eye reaches cephalic mid-line anteriorly, including at least 12 longitudinal files of hexagonal lenses; doublure widest (sag.) mesially, narrowing posteriorly, broadly embayed in posterior outline, covered with ten closely spaced raised terraced ridges subparallel to nearest margins.

Thorax of six segments, subparallel-sided. Axis narrowing backwards, width of sixth ring about half that of the first one. Pleurae correspondingly widening backwards; turned downwards from fulcra, which are arranged roughly parallel to axial furrow; facet triangular, about two-thirds the pleural width in the sixth segment, slightly narrowing (tr.) forwards; pleural furrows deep and wide, narrowing abaxially and extending nearly to truncated distal tips.

Pygidium weakly convex, subparallel-sided, gently arched posteriorly, 57% as long as wide. Axis short (sag.), including one ring and a broadly rounded terminal piece. Postaxial field crossed by sagittal groove which fades out before reaching border furrow. Pleural lobe faceted anterolaterally; indications of anterior three pleurae present in some specimens. Border about 15% pygidial length (sag.), narrowing gently forwards from posterolateral corner. Border furrow shallow.

#### *Meraspid stage*

Degree 2 dorsal shield 3.2mm long. Glabella broadly rounded anteriorly. Palpebral lobe flattened, about 7% of the cranial width (tr.). Eye extends along side of the glabella, reaching cephalic midline anteriorly, including 6 longitudinal files of hexagonal lenses. Thorax of two segments. Transitory pygidium as long as wide. Axis convex, funnel-shaped, with five rings and a terminal piece. Pleural lobe gently downsloping abaxially, with five pleurae which become successively weakly defined posteriorly. Border indistinct.

Degree 3 dorsal shield 3.6mm long. Cranidium broadly rounded anteriorly, gently tapering forwards. Palpebral lobe moderately convex, about 6% the cranial width (tr.), slightly narrowing forwards. Thorax of three segments. Transitory pygidium 80% as long as wide. Axis funnel-shaped, convex, with four rings and a terminus. Pleural lobe slightly abaxially inclined, with four pairs of furrowed pleurae succeedingly becoming better defined anteriorly. Border obscure.

Degree 5 dorsal shield 5.5mm long. Glabella as in holaspids. Thorax of five segments. Transitory pygidium 60% as long as wide. Axis convex, broadly rounded posteriorly, with two rings in addition to a terminal piece. Pleural lobe slightly vaulted adaxial to border, with four pleurae indicated by interpleural ridges. Border narrow (sag.), faintly defined.

#### **Discussion**

The morphological changes from meraspids to holaspids in the present species are as follows:

1. The glabella becomes longer and more narrowly rounded anteriorly;
2. The palpebral lobe is narrow (tr.) and wire-like in adult, but more flattened and wider (tr.) in juvenile specimens;

3. The pygidial border is absent until degree 3, but then appears and gradually becomes more markedly defined and wider (sag.);

4. The visual surface of the eye is enlarged by the increase of longitudinal files of lenses;

5. Axial rings grow wider (tr.);

6. The length/width ratio is much reduced from the transitory to the holaspid pygidium.

The adult specimens of this form agree well with those of *Cyclopyge binodosa* Zhang (1981: 191, pl.72, figs 1–3) from the lower part of the Qilang Formation (Caradoc) of Kanling, Kalpin, northwestern Tarim, Xinjiang, and of *C. cf. recurva* Lu (Zhou and Dean 1986: 758, pl.61, figs 2–5, 7–9, 14) from the upper part (Caradoc) of the Chedao Formation of Chedao, Huanxian, Gansu, northwest China. They are probably conspecific. All of them seem in turn indistinguishable from *C. recurva* Lu in Wang (1962: 53, pl.20, figs 5, 6, 9; 1964: 47, pl.13, figs 14–16; Lu *et al.* 1965: 542, pl.113, figs 8–10; Lu 1975: 173, pl.30, figs 8–12) from the Pagoda Formation (Caradoc) of southern Shaanxi. However, the original specimens of *C. recurva* including the cranidium and transitory pygidia are poorly preserved. In this paper, we follow Zhou and Dean (1986) in referring this form to *C. recurva* with reservation pending a more complete knowledge of the latter. Several species of *Cyclopyge* recently established from the Middle–Upper Ordovician of Uzbekistan (Abdullaev in Abdullaev and Khaletskaia 1970), Turkestan Ridges of southern Tien-Shan (Petrunina in Repina *et al.* 1975) and northern Kazakhstan (Koroleva 1967; 1982) are also closely related to the present form. They include *C. ocula* Abdullaev, *C. abdullaevi* Petrunina, *C. alia* Koroleva, *C. festa* Koroleva, *C. sola* Koroleva, *C. tereki* Koroleva and *C. timida* Koroleva. The tiny likely differences between those central Asian species and the present form might be accounted for in the different preservation and size.

As noted by Zhou and Dean (1986: 760), *C. cf. recurva* is characterized by the anteriorly narrower eyes, a feature distinct from that of the lectotype of *C. mirabilis* (Forbes MS in Salter, 1853) (see Whittard 1952, pl.32, figs 6–8) from the Portrane Limestone (Ashgill) of Ireland. It also bears a superficial resemblance to the Canadian Ashgill species *C. vigilans* (Cooper and Kindle, 1936: 367, pl.52, figs 36, 39, 41–51) from the Whitehead Formation of Percé, Quebec, but differs in the more elongated glabella and narrower (sag.) pygidial border.

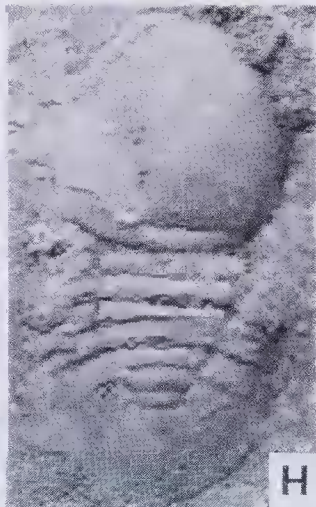
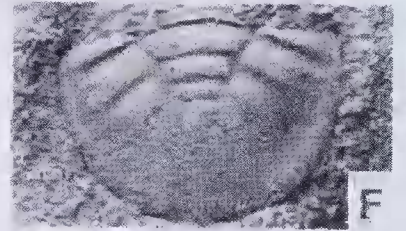
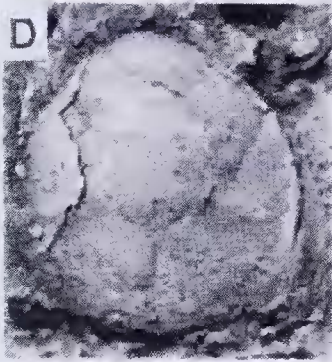
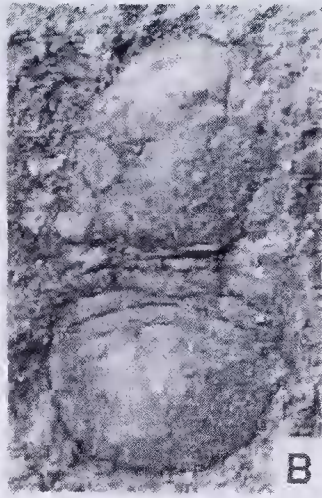
### Genus *Microparia* Hawle and Corda, 1847

#### Type species

*Microparia speciosa* Hawle and Corda, 1847, from the Králův Dvůr Beds (Ashgill), Králův Dvůr, Bohemia.

#### Discussion

We follow Fortey and Owens (1987: 164) in regarding *Heterocyclopyge* Marek, 1961 as a subgenus of *Microparia*. Fortey and Owens also implied that *Microparia* (*Quadratapyge*) Zhou in Zhou *et al.* 1977 might be considered as an independent genus, being characterized by its rectangular pygidium provided with a well defined short pygidial axis and very wide flattened border. The pygidium of the new species *M. (Q.) curva* as described below is typical of *Quadratapyge*, but displays a broadly rounded instead of straight posterior margin. It is therefore closely similar to that of *Heterocyclopyge*, such as the type species *M. (H.) pachycephala* (Hawle and Corda) (Marek 1961: 27, pl.5, figs 9, 10), *M. (H.) nigra* Hörbinger and Vaněk (1985: 60, pl.1, figs 6, 7, pl.2, fig.4) and *M. (H.) abunda* sp. nov. (see below). It differs in the wider (sag.) pygidial border and the more distinct border furrow. The latter feature is, however, shared with *M. (H.) shelvensis* Whittard (1961: 177, pl.24, figs 3) only as





suggested by Fortey and Owens (1987: 167). The wide pygidial border alone is not thought sufficient to warrant separation at the generic level. Therefore, the subgeneric status of *Quadratapyge* is retained in this paper.

### Subgenus *Microparia* Hawle and Corda, 1847

#### *Microparia* (*Microparia*) sp.

Figure 5B

#### Figured specimen

One dorsal shield (lacking librigenae) of degree 2 (NI 120585) from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, locality 1.

#### Discussion

The juvenile incomplete dorsal shield of degree 2, 5.2mm long and 2.7mm wide across the base of the cranidium, shows a well vaulted transitory pygidium with ill-defined border and axis. The cranidium is as long as wide and narrowly rounded anteriorly. It tapers forwards in a parabolic curve. The cranidial outline suggests that the present form is closely allied to *M. (M.) klouceki* (Richter and Richter) (Marek 1961: 42, pl.3, figs 17, 18; also see Whittard 1952: 113, pl.32, fig. 9) and *M. (M.) plasi* Marek (1961: 44, pl.3, figs 22, 23), both from the Dobrotivá Beds (Llandeilo), Bohemia. Judging from the description and illustration given by Marek (1961), the eyes of *M. (M.) klouceki* abut each other, while those of *M. (M.) plasi* may be separated. As librigenae are not known in this form, it seems difficult for the time being to assign it to either of these two species.

### Subgenus *Heterocyclopyge* Marek, 1961

#### Type species

*Cyclopyge pachycephala* Hawle and Corda, 1847, from the Černin Beds (Caradoc), Turbin, Bohemia.

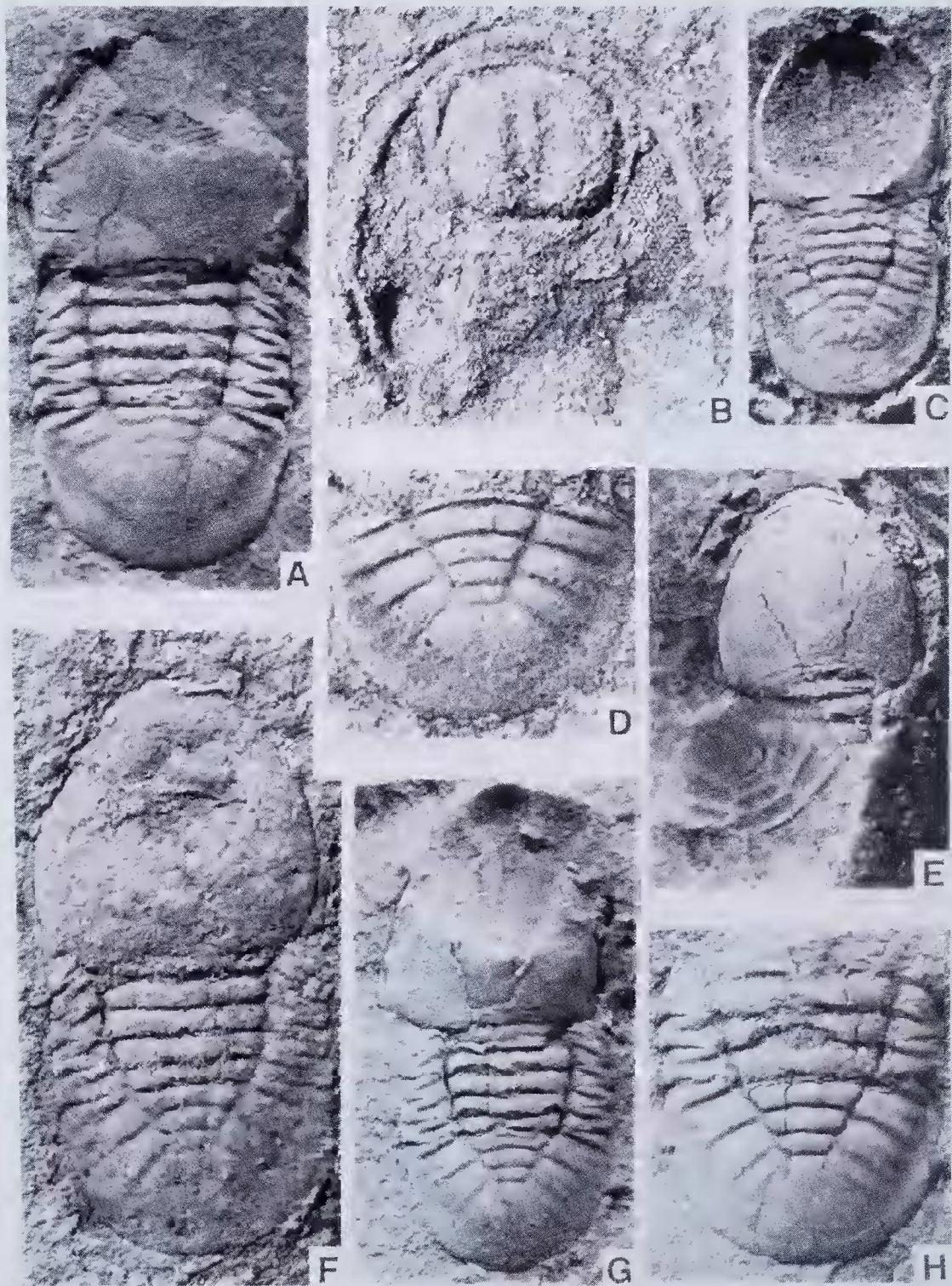
#### *Microparia* (*Heterocyclopyge*) *abunda* sp. nov.

Figures 5C, D, F–I, 6A–H, 7A, C, E, H

#### Etymology

Latin *abundus*, *a*, *um*, abundant, referring to the specimens of this new species which outnumber those of other cyclopygids in our collection.

◀ **Figure 5** A, E, *Pricyclopyge* cf. *binodosa longicephala* Klouček, 1916, from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, Loc.1; A, dorsal shield lacking librigenae, degree 1, latex cast, NI 120574, x15; E, dorsal shield lacking librigenae, degree 2, latex cast, NI 120575, x10. B, *Microparia* (*Microparia*) sp., from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, Loc.1, dorsal shield lacking librigenae, degree 2, NI 120585, x10. C, D, F–I, *Microparia* (*Heterocyclopyge*) *abunda* sp. nov., all from the *Nemagraptus gracilis* Zone, except G from the *Climacograptus bicornis* Zone, of the middle part of the Charchaq Group, Loc.1; C, dorsal shield lacking librigenae, degree 1, paratype, NI 120586, x15; D, cranidium, paratype, NI 120587, x10; F, pygidium, paratype, NI 120588, x10; G, dorsal shield lacking librigenae, paratype, NI 120589, x6; H, dorsal shield lacking librigenae, paratype, latex cast, NI 120590, x6; I, incomplete dorsal shield, paratype, NI 120591, x4.



## Holotype

Incomplete dorsal shield, NI 120592 (Figure 6A), from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, locality 1.

## Paratypes

Five incomplete dorsal shields (NI 120590, 120591, 120597, 120598, 120601), two cranidia (NI 120587, 120602), one cranidium and pygidium (NI 120596), one pygidium (NI 120588), two pygidia with attached thoracic segments (NI 120599, 120603), two incomplete meraspid dorsal shields of degree 1 (NI 120586) and degree 4 (NI 120594), and one degree 4 transitory pygidium (NI 120595) from the *Nemagraptus gracilis* Zone, and one incomplete dorsal shield (NI 120589), one cephalic doublure attached with hypostoma (NI 120593), and one pygidium and thorax (NI 120600) from the *Climacograptus bicornis* Zone, of the middle part of the Charchaq Group, locality 1.

## Diagnosis

A species of *M. (Heterocyclopyge)* with straight-sided pygidium. Pygidial axis 51–55% the length (sag.) of pygidium, with three well defined rings and a triangular weakly delimited terminal piece. Pleural lobes with three pairs of furrowed pleurae.

## Description

### *Holaspid specimens*

Adult dorsal shield 8–18mm long in the collection; cranidium 46–48%, thorax 20–24% and pygidium 29% the exoskeletal length. Cranidium about as long as wide. Glabella convex, parabolic in outline, narrowly rounded anteriorly (Figure 6F), slightly convex backwards posteriorly, with maximum width attained at 38% the glabellar length in front of the posterior margin; a tiny median tubercle situated slightly posterior to the mid-length (Figure 7E). Palpebral lobe rim-like, probably meeting in front of the glabella. Posterior area of fixigena tiny, elongated-triangular. Librigenae united; cephalic doublure narrows backwards gently, surface covered with raised terrace lines subparallel to its margin; eyes poorly preserved, but indications (Figure 5G) suggest that they may probably closely approach the mid-line in front. Hypostoma (Figure 6B) trapezoid-shaped, broadly rounded anteriorly, about 80% as long as wide; middle body moderately convex, with a median ridge well defined by deep and broad longitudinal furrows on either side; anterior wing small, triangular; border furrow deep and wide; border convex, almost even in width.

Thorax of five segments, subparallel-sided (Figure 5I). Axis wide (tr.), gently convexly curved laterally, tapering moderately backwards over posterior three rings, occupying 60% the thoracic width anteriorly and 50% posteriorly; articulating half ring short (sag.), ridge-like. Axial furrow deeply incised (Figure 6A,F,H). Pleurae slightly widens backwards over the

◀ **Figure 6** A–H. *Microparia (Heterocyclopyge) abunda* sp. nov., all from the *Nemagraptus gracilis* Zone, except B from the *Climacograptus bicornis* Zone, of the middle part of the Charchaq Group, Loc.1: A, incomplete dorsal shield, holotype, NI 120592, x6; B, cephalic doublure with attached hypostoma, paratype, latex cast, NI 120593, x10; C, incomplete dorsal shield, degree 4, paratype, NI 120594, x8; D, transitory pygidium, degree 4, paratype, NI 120595, x15; E, cranidium and external mould of pygidium, paratype, NI 120596, x8; F, dorsal shield lacking librigenae, paratype, latex cast, NI 120597, x10; G, dorsal shield lacking librigenae, paratype, NI 120598, x10; H, pygidium and attached three thoracic segments, paratype, NI 120599, x7.

posterior three segments. Each pleura bluntly pointed distally (Figure 5I); fulcrum fairly close to the axial furrow; facet triangular, wide (tr.); pleural furrow deep and wide, widening adaxially.

Adult pygidium 3.3–9mm in width and 2.3–6mm in length, semicircular in outline (Figure 6H), straight-sided laterally, 63–70% as long as wide. Axis occupying 51–55% pygidial length and 40–50% pygidial width at anterior margin, slightly convex, funnel-shaped, entire, with three well defined rings and a faintly shown triangular terminal piece. Pleural lobes moderately declined towards border furrow abaxially, with three pairs of pleurae weakly outlined by shallow interpleural furrows, which successively become weaker posteriorly; pleural furrows broad and distinct, but only the first pair being deeply incised, delimiting a widely faceted anterior half pleura. Border slightly adaxially declined laterally, feebly bent down mesially, 10–20% pygidial length (sag.), sharply narrowing forwards from posterolateral pygidial corners. Border furrow shallow and broad, more faintly defined sagittally. Doublure broad (Figure 6A), up to 30% the pygidial length (sag.), narrowing forwards laterally, covered with fine terrace lines subparallel to the border furrow.

#### *Meraspid specimens*

Degree 1 dorsal shield (lacking librigenae) (Figure 5C) 4.5mm long and 2.3mm wide. Cranium shows a proportionally slightly wider (tr.) palpebral lobe than in adult. Transitory pygidium as long as wide, parallel-sided, broadly rounded posteriorly. Axis funnel-shaped, divided into seven rings and a terminal piece. Axial furrow shallow, becoming shallower backwards. Pleural lobes include seven pairs of furrowed pleurae; the posterior three pairs of interpleural furrows very weak. Border ill-defined.

Degree 4 dorsal shield (lacking librigenae) (Figure 6C) 6.3mm in length and 3.1mm in width. Cranium almost indistinguishable from the adult. Thorax of four segments, parallel-sided; axis wide (tr.), well defined by deep and broad axial furrows, which are gently curved laterally. Transitory pygidium 75% as long as wide, straight-sided laterally, broadly rounded posteriorly. Axis with four well defined rings and a weakly outlined terminal piece in addition to a ridge-like anterior half ring. Pleural lobe slightly vaulted, provided with four pleurae; pleural furrows distinct; interpleural furrows weak; anterior half pleura convex, broadly faceted. Border 10% the pygidial length sagittally, narrowing forwards, defined by shallow and broad furrow, which becomes fainter mesially.

#### Discussion

The new species bears a great resemblance to the type species *M. (H.) pachycephala*, and *M. (H.) nigra* from the Dobrotivá Beds (Llandeilo), Praha-Libeň, Bohemia, in many respects, especially in the shape of the pygidium. The type species differs in the longer pygidium (length/width ratio 74–89% vs. 63–70%), the longer axis (50% vs. 51–55% pygidial length) with more weakly incised ring furrows but better defined and posteriorly more rounded terminal piece, and the effaced pleural lobe. *M. (H.) nigra* is closely related to *M. (H.) pachycephala* with regard to the characters of the pygidial axis and pleural lobe. According to Hörbinger and Vaněk (1985: 60) the length/breadth index of the pygidium is 74%, but judging from the dimensions of the holotype given in the same paper, the figure should be greater than 75%. In this regard, therefore, the diagnostic feature of *M. (H.) nigra* appears to fall within the range of variation of the type species, indicating that both the Bohemian species might be synonymous.

The pygidium of *M. (H.) shelvensis* Whittard from the Stapeley Volcanic Group, Linley, Shropshire, England has three well marked axial rings, a weakly demarcated triangular terminal piece, three pairs of pleurae and a wide (sag.) doublure (less than 30% the pygidial length in the holotype according to Rushton and Hughes 1981: 634) as in that of the new species, but it is proportionally slightly short (60% as long as wide) with more rounded lateral margins (cf. straight-sided). The cephalon of the English species recalls that of *M. (H.) abunda* sp. nov., but possesses a glabella more bluntly rounded anteriorly, and, as pointed out by Whittard (1961: 178), its eyes reach only almost to the level of the glabellar front.

The featureless cranium, the holotype of *Cyclopyge angustata* Cooper and Kindle (1936: 367, pl.53, figs 26, 34), from the Whitehead Formation, Percé, Quebec, Canada, is similar to the present species in outline, but the presence of its glabellar anterior tongue suggests that the eyes may well be separated in front of the glabella. As no pygidium has been referred to that Ashgill form, its generic assignment is still in doubt. However, a small pygidium identified as *Cyclopyge* sp. (Cooper and Kindle 1936: 367, pl.52, fig.14) might belong to *C. angustata* as suggested by the authors. If this were the case, *C. angustata* would be referable to *M. (Heterocyclopyge)* as the pygidium is almost identical with that of this species.

The incomplete size series as described above indicates that the morphological changes of the new species from the meraspids to the holaspids may include the deepening of the pygidial border furrow, the broadening of the pygidium, and the narrowing of the palpebral lobe. During the holaspid stage, the pygidial border gradually becomes wider and better defined, but the axial and ring furrows seem to become shallower.

### **Subgenus *Quadratapyge* Zhou in Zhou et al., 1977**

#### **Type species**

*Microparia (Quadratapyge) latilimbata* Zhou in Zhou et al., 1977, from the Modaoxi Formation (Caradoc), Modaoxi, Taojiang, Hunan, S China.

#### ***Microparia (Quadratapyge) curva* sp. nov.**

Figure 7D, F,I

#### **Etymology**

Latin *curvus*, *a*, *um*, curved, referring to the backwardly arched posterior margin of the pygidium.

#### **Holotype**

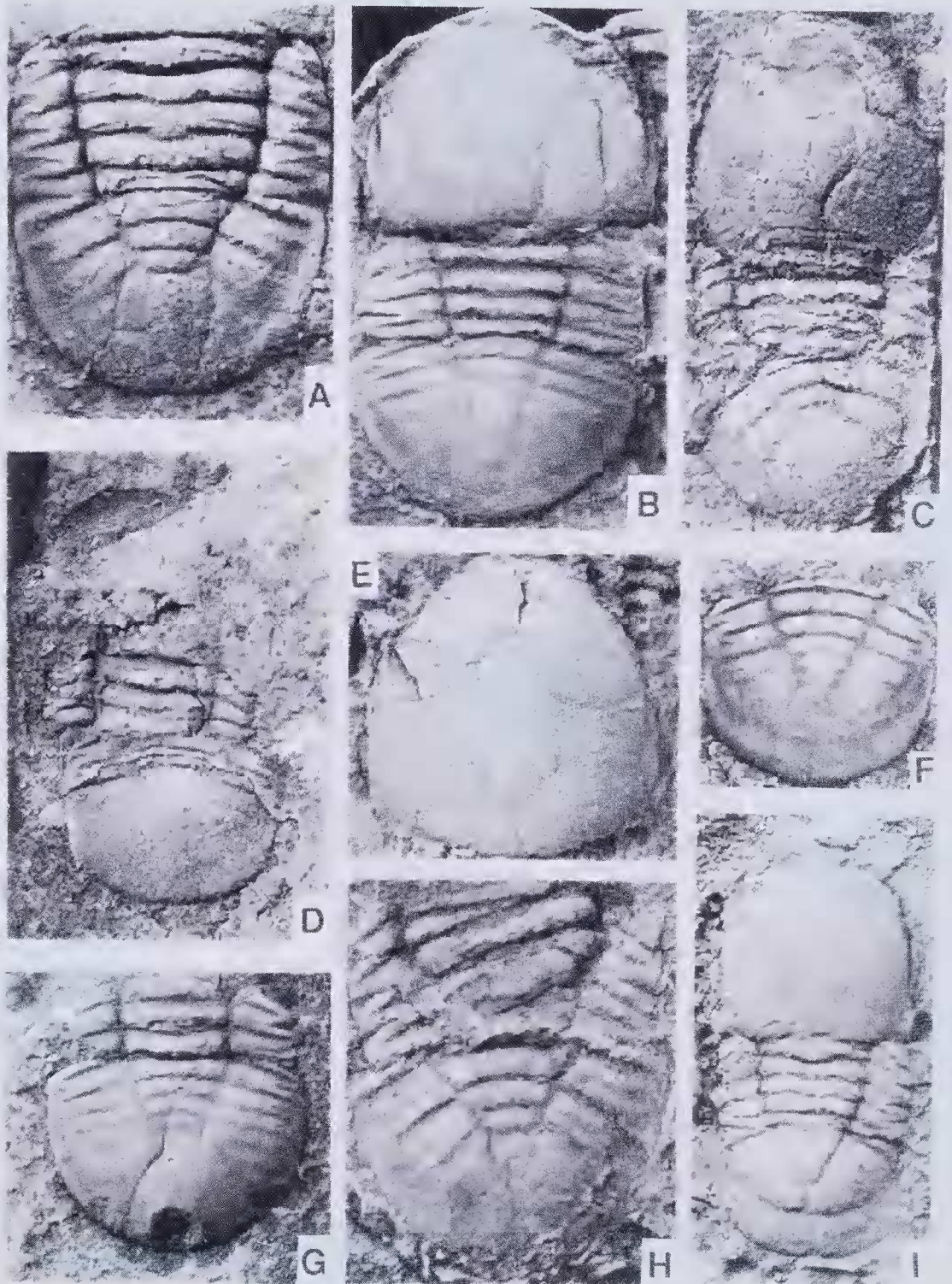
Dorsal shield lacking librigenae, NI120608 (Figure 7I), from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, locality 1.

#### **Paratypes**

One transitory pygidium of degree 3 with attached thorax and cephalic doublure (NI 120606) and one transitory pygidium of degree 3 (NI 120607), from the same horizon and locality as the holotype.

#### **Diagnosis**

A species of *M. (Quadratapyge)* with pygidium broadly rounded posteriorly. Axis conical in outline. Postaxial groove extending sagittally and reaching border furrow.



## Description

### *Holaspid specimens*

Dorsal shield elliptical in form, cranidium 48%, thorax 20% and pygidium 32% of the exoskeletal length. Glabella convex, parabolic, widely arcuate anteriorly, slightly longer than wide, with a tiny median tubercle located at 40% the glabellar length from rear. Axial furrow deeply incised adaxial to palpebral lobe, shallower posteriorly adaxial to the small triangular posterior area of fixigena. Palpebral lobe narrow (tr.), strip-like, gently narrowing forwards.

Thorax of five segments, parallel-sided. Axis wide (tr.), convex, tapering backwards moderately from first to third but more rapidly from third to fifth rings, occupying 55% thoracic width (tr.) anteriorly and 40% posteriorly. Pleurae narrowing forwards; pleural furrows wide and deep, widening adaxially; fulcra much closer to the axial furrows; each pleura bluntly pointed distally, with broad (tr.) triangular facet.

Pygidium subrectangular in outline, broadly rounded posteriorly, 68% as long as wide. Axis moderately convex, conical in shape, occupying 47% sagittal length and 32% anterior width of pygidium, well defined by distinct axial furrows, with three faintly defined rings and a terminal piece in addition to a ridge-like articulating half ring. Postaxial groove extending from axial tip to border furrow. Pleural lobe slightly vaulted; anterior half pleura raised, narrowing adaxially, facet occupying 70% the anterior pleural width; first pair of pleural furrows deep, other two very faint though traceable. Border crescentic in shape, straight-sided, 33% pygidial length sagittally, narrowing slowly abaxially to posterolateral pygidial corner, from there then sharply tapering forwards, well defined by distinct semicircular-extended border furrow.

### *Meraspid specimens*

Cephalic doublure, as exhibited in an incomplete dorsal shield of degree 3 (Figure 7D), broadly rounded anteriorly, widest at sagittal line, narrowing backwards, covered with raised terrace lines subparallel to its posterior margin. Transitory pygidium of degree 3, 2.9–3.2mm wide and 2.4–2.9mm long, parallel-sided, broadly rounded posteriorly. Axis conical, including five rings which successively become faintly defined posteriorly, a tiny terminus and a ridge-like anterior half ring. Pleural lobe faceted anterolaterally, with five pairs of pleural and interpleural furrows, of which the posterior two are only weakly developed. Border 25% length (sag.) of the transitory pygidium, narrowing anteriorly. Border furrow very shallow or poorly defined. Doublure slightly wider than, or of almost equal width as, the border.

◀ **Figure 7** A, C, E, H, *Microparia (Heterocyclopyge) abunda* sp. nov., A from the *Climacograptus bicornis* Zone, C, E, H from the *Nemagraptus gracilis* Zone, of the middle part of the Charchaq Group, Loc.1; A, pygidium and thorax, paratype, NI 120600, x10; C, dorsal shield, paratype, NI 120601, x10; E, cranidium, paratype, NI 120602, x6; H, pygidium and thorax, paratype, NI 120603, x8. B, G, *Degamella cf. princeps* (Barrande, 1872), from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, Loc.1; B, dorsal shield lacking librigenae, degree 4, NI 120604, x8; G, transitory pygidium and attached thorax, degree 2, NI 120605, x10. D, F, I, *Microparia (Quadratapyge) curva* sp. nov., from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, Loc.1; D, transitory pygidium attached with thorax and cephalic doublure, degree 3, paratype, NI 120606, x10; F, transitory pygidium of degree 3, paratype, NI 120607, x10; I, dorsal shield lacking librigenae, holotype, NI 120608, x8.

## Discussion

Only two species have been assigned to *M. (Quadratapyge)*, the type species *M. (Q.) latilimbata* Zhou (in Zhou *et al.* 1977: 230, pl. 69, figs 14–16), and *M. (Q.) chedaoensis* Zhou and Dean (1986: 761, pl. 61, figs 6, 10, 11, 13, 16) from the lower part (late Llandeilo-basal Caradoc) of the Chedao Formation, Chedao, Huanxian, Gansu, northwest China. Both differ from the new species in the straight posterior pygidial margin, the broadly rounded posterior end of axis and the absence of a postaxial groove. Furthermore, the pygidial axis is much wider (40–50% the pygidial width anteriorly) and the median glabellar tubercle is more forwardly placed (in front of the glabellar centre) in the type species. The pygidial axis occupies 33% the pygidial width anteriorly in *M. (Q.) chedaoensis*, a feature shared with the present species, but its pygidial border is narrower (sag.) (20% the pygidial length) and the median tubercle is situated in the centre of the glabella. The pygidial border furrow is much more faintly defined, the axial furrow is shallower, and the postaxial groove is absent in the transitory pygidium of this new species as compared with the adult specimens.

## Genus *Degamella* Marek, 1961

### Type species

*Aeglina princeps* Barrande, 1872, from the Dobrotivá Beds (Llandeilo), Svata Dobrotivá, Bohemia.

### *Degamella cf. princeps* (Barrande, 1872)

Figure 7B, G

### Figured specimens

One dorsal shield (lacking librigenae) of degree 4 (NI 120604), and one degree 2 transitory pygidium and thorax (NI 120605), from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, locality 1.

## Description

### *Meraspid specimens*

Dorsal shield of degree 4, 8.8mm long, oval in outline. Glabella gently convex, subcircular in form, wider than long, extremely broad-rounded anteriorly, with an elongated median tubercle situated at 60% the sagittal length from the posterior margin. Axial furrow shallow posteriorly, deep adjacent to palpebral lobe. Palpebral lobe band-like, narrowing forwards, posteriorly placed, about 40% the glabellar length. Posterior area of fixigena tiny, triangular. Thorax of four segments, subparallel-sided. Axis convex, half the thoracic width (tr.) anteriorly, tapering backwards. Axial furrows deep. Pleurae broadly faceted abaxially, distal ends bluntly pointed. Pleural furrows deep and wide. Transitory pygidium weakly vaulted, 64% as long as wide, semicircular in outline. Axis flatly convex, conical, 76% the length and 22% the anterior width of the pygidium, entire, divided into six rings and a narrowly rounded terminal piece, of which only anterior two are well defined. Pleural lobes including three pairs of feebly marked pleurae in addition to two well demarcated anterior future thoracic segments. Border flattened. Border furrow shallow and wide. Doublure about 19% the length of the transitory pygidium sagittally, narrowing gently abaxially, covered with subparallel and closely spaced terrace lines, anterior margin convexly arched forwards along the sagittal line and almost reaching the terminal end of the axis.



Degree 2 transitory pygidium 2.7mm long, 77% as long as wide. It is more vaulted, with an axis funnel- rather than cone-shaped, and the axial, border, and pleural furrows are more weakly defined on the true pygidium than in degree 4.

## Discussion

*D. princeps* (Barrande) was described in detail by Marek (1961: 46, pl.4, figs 1–7), but no ontogenetic series has been established except a specimen of degree 3 (Marek, 1961:48), which has been recorded by Barrande (1872, pl.14, figs 6, 7). It shows an oval dorsal shield with a subcircular, anteriorly very widely rounded glabella, and an indistinctly segmented pygidium, in contrast to an elliptical carapace with an elongated, anteriorly narrowing rounded glabella and almost smooth pygidium both in axis and pleural lobe in mature specimens, but almost identical with the present degree 4 specimen. Moreover, both forms share a very distinctive character in cyclopygids – the mesially upcurved pygidial doublure. We therefore consider the present specimens either referable or at least very close to the type species of *Degamella*. Marek (1961) separated the type species into two subspecies, that is, *D. princeps princeps* and *D. princeps praecedens* (Klouček 1916), but the latter, though from an earlier horizon (the Llanvirn Šárka Beds) in Bohemia, is in fact no different from the former, as indicated by Fortey and Owens (1987: 160).

The meraspid degree 3 and 5 and young holaspid dorsal shields of *D. nuda* (Whittard, 1961: 180, pl.24, figs 5–10) have been well described and figured from the Llanvirn of Shropshire, England. It is interesting to note that the immature specimens also exhibit a shorter carapace and a broader glabella as in the type species and the present form, suggesting that the elongation of the exoskeleton and glabella may be the most prominent morphological change which took place during the ontogeny of the known species of *Degamella*.

## Genus *Sagavia* Koroleva, 1967

### Type species

*Sagavia felix* Koroleva, 1967, from the Llandeilo of northern Kazakhstan.

### *Sagavia felix* Koroleva, 1967

Figure 8A–J

*Sagavia felixa* Koroleva, 1967: 82, pl. 10, figs 2–4.

*Sagavia felixa* Koroleva, Abdullaev, 1972: 107, pl. 46, fig. 9.

*Sagavia felixa* Koroleva, 1982: 127, pl. 26, fig. 7.

*Sagavia* sp.1, Koroleva, 1982: 130, pl. 26, fig. 7 (as pl. 10, fig. 3 of Koroleva, 1967)

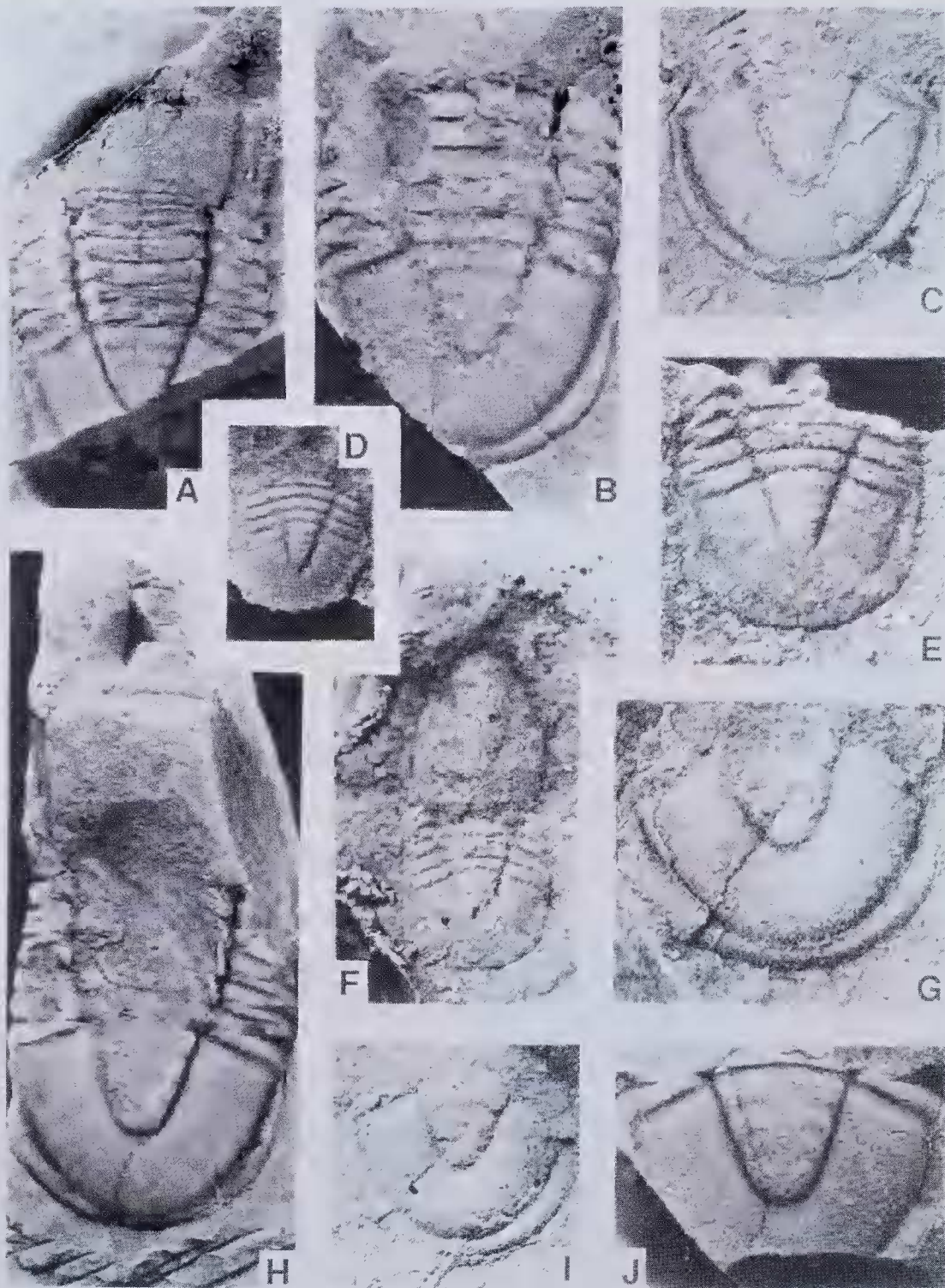
*Sagavia felix* Koroleva, Fortey and Owens, 1987: 177.

### Holotype

Incomplete dorsal shield, K-98-2, figured Koroleva (1967, pl.10, fig.2; 1982, pl.26, fig.4), from the Tselinograd horizon (Llandeilo), right bank of the Sagi River, northern Kazakhstan.

### Figured specimens

One fragmentary dorsal shield (NI 120609), one pygidium attached with incomplete thorax and cephalic doublure (NI 120616), one pygidium and thorax (NI 120610), four pygidia (NI



120611, 120615, 120617, 120618), one degree 1 dorsal shield (lacking librigena) (NI 120614) and two degree 1 transitory pygidia (NI 120612, 120613) from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, locality 1.

## Description

### *Holaspid specimens*

Cranidium incompletely preserved. Glabella broadly arcuate laterally, well defined by deep and broad axial furrows. Palpebral lobe long, narrow (tr.), strip-like. Posterior area of fixigena tiny, triangular. Librigena occupied mainly by large eyes; doublure wide (sag.), narrowing backwards, covered by subparallel fine terrace lines. Hypostoma fragmentary, but indicating an outline of reversed trapezoid; surface overspread with terrace lines subparallel to the nearest margin.

Thorax of five segments, broadly curved but almost parallel-sided laterally. Axis gently tapering backwards, 50% and 40% the thoracic width on the first and fifth segments respectively. Pleurae narrowing forwards; each pleura extending abaxially for about 30% its width to fulcrum, then curving gently downwards into a truncated distal extremity; pleural furrow wide and deep; facet wide (tr.), triangular.

Pygidium semioval in form, moderately vaulted, 51–81% as long as wide. Axis entire, tapering backwards, rounded posteriorly, 45–55% the length and 37–44% the width of pygidium, consisting of three rings, a rounded terminal piece and an articulating half ring; ring furrows shallow and wide. Axial furrow deep and broad. Pleural lobes decline gently towards the border furrow; anterior half pleura raised, widening abaxially, faceted anterolaterally, well defined by deep first pair of pleural furrows; faint indications of second and third pairs of pleural furrows present only on internal moulds. Border convex, widest at posterolateral corner, from where it narrows anteriorly and posteriorly. Border furrow broad and deeply incised.

Surface of testaceous thorax and pygidium covered with wide-spaced raised lines, which are transverse on axis, subparallel to lateral margin on thoracic pleurae, and curved convexly forwards on pleural lobe of pygidium.

### *Meraspid specimens*

Degree 1 dorsal shield (Figure 8F) 4.9mm long. Glabella gently arcuate laterally, narrowly rounded anteriorly, 74% as long as wide. Palpebral lobe long, wire-like, slightly narrowing forwards. Thorax of one segment. Pleura faceted, shortly pointed abaxially, with deep and wide pleural furrow. Transitory pygidium 1.8–2mm in length, as wide as long, parallel-sided, broadly rounded posteriorly. Axis about 70% pygidial length, tapering backwards sharply, composed of four well marked and three faintly defined rings and a narrowly rounded terminus. Axial furrow becomes shallower posteriorly. Pleural lobe slightly vaulted, with seven pairs of pleural and six pairs of interpleural furrows; posterior two pairs of pleural and

◀ **Figure 8** A–J, *Sagavia felix* Koroleva, 1967, from the *Nemagraptus gracilis* Zone of the middle part of the Charchaq Group, Loc.1; A, incomplete dorsal shield, NI 120609, x4; B, pygidium and attached thorax, NI 120610, x5; C, pygidium, NI 120611, x4; D, E, transitory pygidia of degree 1, NI 120612, 120613, x10, x15; F, dorsal shield lacking librigenae, degree 1, NI 120614, x10; G, pygidium, NI 120615, x8; H, pygidium attached with incomplete thorax and cephalic doublure, NI 120616, x4; I, pygidium, NI 120617, x5; J, incomplete pygidium, NI 120618, x5.

interpleural furrows only faintly shown. Border defined by shallow furrow, narrow (sag.), widest posterolaterally, narrowing anteriorly to, and confluent with, anterior half pleura of fifth pleura.

### Discussion

Since the type species *S. felix* was established by Koroleva (1967), a single pygidium has subsequently been referred to it by Abdullaev (1972) from the late Ordovician of the Bukantau Mts, Uzbekistan. The new material agrees well with the original specimens, and is also considered as referable to the species. The pygidium of the holotype is 77% as long as wide with the axis about 55% the pygidial length. The figures fall within the range of variation shown in our specimens.

Four other species from Central Asia have been assigned to the genus *Sagavia*: *S. modica* Koroleva (1967: 83, pl.10, figs 5, 6; 1982:129, pl.26, figs 5, 6), *S. novakellaformis* Koroleva (1982: 30, pl.26, fig.9) and *S. heterocyclopygeformis* Koroleva (1982: 32, pl.26, fig.10) from the Middle Ordovician (Llandeilo-Caradoc) of northern Kazakhstan, and *S. elongata* Petrunina (in Repina *et al.* 1975: 191, pl.33, figs 17, 20–23) from *Kielanella-Tretaspis* beds of Ulugtay District, south Tien-Shan. All these species were separated largely on the basis of different proportions of the pygidial width to length and the pygidial axis to the pygidium, but, as noted by Fortey and Owens (1987: 179), they all have well defined pygidial axes and posterolaterally widening pygidial borders as in the type species. In specimens of these four species, the length/width ratio of the pygidium varies from 60% to 80%, and the length of the pygidial axis is 50–58% the pygidial length, almost comparable with the range of intraspecific variation in *S. felix* as indicated by the present material. It seems likely that these Central Asian species may be either a group of species closely related to, or even conspecific with, the type species.

*Sagavia glans* Fortey and Owens (1987: 177, Fig. 54a–c) from the Pontyfenni Formation (late Arenig), Pontyfenni, South Wales has been considered as a primitive form by the authors; it is characterised by the pygidial axis being poorly defined posteriorly and the pygidial border steadily widening posteriorly.

Judging from the present material, morphological changes that took place during the ontogeny of *S. felix* are minimal, including only the deepening of the border furrow and posterior axial furrow of the pygidium. Following the successive release of the anterior segments to the thorax, the transitory pygidium becomes proportionally shorter (sag.); it is 45% the exoskeletal length in the meraspid degree 1, but in the holaspid pygidium the corresponding figure is 36%.

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